Biology of *Trypophloeus striatulus* (Coleoptera: Scolytidae) in Feltleaf Willow in Interior Alaska

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ABSTRACT The biology of the willow bark beetle, *Trypophloeus striatulus* (Mannerheim) was studied in its primary host, *Salix alaxensis* (Andersson) Coville, at 28 locations in Alaska, and in the laboratory. Most broods transformed to adults before fall, emerged, and excavated solitary chambers in the bark, where they passed over-winter before becoming sexually mature in spring. Emerged adults walked on the bark for protracted periods, lacking any disposition to fly. This behavior contributes to reinfesting the stem, downward for several generations, thereby conserving a susceptible host (limited resource). A fungus, *Cytospora* sp., most likely *chrysosperma* (Person) Fries, was present in stems infested by the beetles. Adults usually chose a lenticel as a site for excavating a chamber, tapping the surface with their antennae, and were possibly attracted there by odor emitted by fungus-infected, underlying tissue. Egg galleries are cavelike. Eggs are exceptionally large relative to the adult, and are laid in a cluster averaging ≈20 per female. Larvae pass through three instars, feeding en masse in the first instar, then becoming solitary. Their mines contain almost entirely excrement, lacking fragments of phloem common in galleries of most bark beetles. Pupation occurs in a cell, excavated by the larva, which usually etches the xylem. A bird preys on over-wintering larvae; otherwise the beetle has few natural enemies. An unidentified endoparasitic nematode occurs in the hemocoele of adults. Commensals in galleries include several undescribed mites, and maggots of the dipterous family Sepsidae. The ecology of feltleaf willow and population dynamics of the beetle are discussed.

KEY WORDS Scolytidae, *Trypophloeus*, *Cytospora*, feltleaf willow

WILLOWS (*Salix* spp.) are the most genetically diverse woody plants in Alaska, consisting of 29 species (Viereck and Little 1972). They are critically important to the distribution and survival of moose and ptarmigan, they are an early seral stage in the colonization of old riverbeds and lakebeds, and are a dominant feature of extensive areas of tundra.

Feltleaf willow is an especially important species, and is abundant along interior rivers where it is used heavily as habitat and browse by moose (Sutter and Gillingham 1990). Feltleaf willow occurs as a pioneer species on freshly deposited gravel bars on meandering rivers. Such bars develop on inside turns opposite cut banks. Dense young stands develop within the flood zone forming discontinuous narrow bands. They are subject to injury from ice jams and, locally, from moose browsing and other agents. As the river continues to cut away the outside bank and new gravel accumulates on the inside bend, established feltleaf willows gradually mature and are replaced eventually by alder and poplar hastened by agents such as *Cytospora* sp. and the willow bark beetle, *Trypophloeus* (=*Cryphalus*) *striatulus* (Mannerheim), that lessen their vigor.

In July 1992 and 1993, I flew on the Forest Service forest insect aerial survey, covering major drainages from the Yukon, Canada border, west to Dillingham, and north from Lake Clark to Nome and Bettles. That survey and observations at additional locations on visits to Alaska since 1967 established that *T. striatulus* is commonly involved in killing stems of feltleaf willow over extensive areas. *Trypophloeus striatulus* is perhaps the most important willow-infesting insect in Alaska because of its involvement in killing stems, particularly those of feltleaf willow, and because of its wide distribution. Outbreaks of defoliating insects such as a willow leafblotch miner, *Micrurapteryx salicifoliella* (Chambers), (Furniss et al. 2001) are visually more spectacular but are not so persistent and normally have no apparent lasting effect. Furthermore, other stem-infesters, mainly a buprestid, *Agrilus politus* (Say), and a cerambycid, *Saperda* sp., most likely *populnea* L., are localized and therefore less important.

Trypophloeus striatulus occurs in boreal North America from Alaska to Nova Scotia, and in Idaho (uncommonly), Utah, Colorado, and Minnesota (Bright 1976, Wood 1982). *Cryphalus striatulus* was described from "Kenai" (Alaska) by Mannerheim (1853) but the type is not in the Helsinki Museum and presumed lost (Wood 1982). Before I collected it in feltleaf willow, *Salix alaxensis* (Andersson) Coville, at Brushkana Campground (east of Cantwell) in 1967,

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the beetle was not known with certainty from Alaska and its only known hosts were *Salix scouleriana* Barratt and *Alnus crispa* (Ait.) Pursh (Wood 1982). A related species, *Trypophloeus populi* Hopkins, has been studied in quaking aspen, *Populus tremuloides* Michaux, in Utah (Petty 1977). [According to Hamilton (1894), *Cryphalus striatulus* Mannerheim was described (1853) from "Kenai" (Alaska) consisting of "two varieties". That wording and the primitive state of knowledge at that time of existent species of Scolytidae and their taxonomy compounded by loss of the types (Wood 1982) puts the Kenai record in doubt. The author looked for this beetle on the Kenai Peninsula in 1996 and, because of the lack of a satisfactory host, concluded that it is unlikely to occur there.]

Reported herein are observations during 1996 and 1997 of the beetle's biology, hosts, and factors associated with susceptibility of willows to infestation.

Materials and Methods

From 23 June to 3 July 1996, I examined willows on the Kenai Peninsula and around Cantwell, Fairbanks, Paxson, and the Denali Highway. From 27 August to 11 September, I explored the roads around Nome, the Niukluk River below Council, and the Kobuk River above Kobuk Village. On those visits, I collected all stages of *T. striatulus*, and photographed infested willows that displayed browsing damage or senescence, beetle galleries, and symptoms of infection by a lesion-forming fungus (*Cytospora* sp.). I also collected infested stem sections from 50 representative willows for rearing and periodic examination at Moscow, ID, to study adult and larval behavior and to describe life stages.

During 1997, 78 representative stem sections of 3–9 cm diameter and 43 m total length were collected from Cantwell, Seward Peninsula and Selawik National Wildlife Refuge (SNWR) at nine times between 3 June and 29 September, and were shipped to Moscow, ID. Thereafter, the behavior of beetles (including walking, mating, boring) was observed periodically and 111 galleries were excavated at intervals of time to study their characteristics, brood production, life stages, seasonal history, and associated organisms. Additional comparative biological data and specimens were obtained in 1997 at Cantwell, Seward Peninsula, and SNWR during 1–14 June, and from the Kobuk River and SNWR during 26 August-10 September. Fifty beetles freshly emerged from bark were mounted on stubs and viewed by scanning electron microscopy (SEM) to detect fungus spores on their integument. Voucher specimens are deposited in the W. F. Barr Entomological Museum, University of Idaho, Moscow, ID.

Results

Distribution. The beetle was collected and observed at the following locations: Seward Peninsula (Niukluk, Sinuk, Penny, Pilgrim, Nome, and Cripple Rivers); Unalakleet River; SNWR (Selawik, Kugarok, and Tagagawik Rivers); Kobuk River; Noatak River; North Slope rivers including Colville, Anatuvik, Canning, and Kongakut Rivers); Fairbanks (Goldstream R.), McKinley National Park, Cantwell, 40 km and 60 km south of Cantwell, Denali Highway (Brushkana Campground, Maclaren River, Rock Creek, Tangle Lakes), Paxon, 43 km north of Paxon, Porcupine River, Ft. Yukon, Bettles, and Galena. The collection from Canning River (Shublik Spring, Lat. N 69° 30′) is perhaps the northernmost record of any scolytid.

Host Relationships. *Salix alexensis* was the common host in all areas visited. Other new, but incidental, hosts included: *Salix arbusculoides* Andersson, *Salix glauca* L., *Salix planifolia* Pursh ssp. *pulchra* (Chamissio), and *Salix bebbiana* Sargent. The beetle was prevalent in feltleaf willow that had been browsed heavily by moose (Fig. 1A). In other areas it occurred in usually larger older trees (Fig. 1B) often showing no sign of predisposing injury although damage from spring ice jams was common where that occurred. In most instances, dying of stems infested with *T. striatulus* stimulated sprouting of replacement stems. That was less true of large or old trees (up to 6 m height, 18 cm basal diameter) having a single stem, apparently because they lacked sufficient reserves to provide energy for sprouting.

Seasonal History. Eggs were present in the field throughout June until mid July. The earliest dates on which each instar was observed were: instar I, 18 June; instar II, 8 July; instar III, 12 July. Instar III either pupated beginning 17 August or over-wintered, apparently depending upon time since they originated as eggs. New adults began to appear 23 August and over-wintered solitarily in the bark.

Description of Life Stages. Eggs were translucent white and oblong and were 0.69 mm (0.65–0.78 mm) long and 0.36 mm (0.34–0.41 mm) wide (n = 17). Three instars occur (Table 1). They are rather slender with a head one half the body width. Head capsule of third instars is more sclerotized and darker yellowish brown than the previous instars. Mandibles are outlined blackish. Prepupal larvae evacuate their gut and are snow white. Pupae were white with eyes and mandibles turning blackish-brown when mature. Female adults were 2.2 mm (2.0–2.4 mm) long; males were 2.0 mm (1.8–2.3 mm) long, based on 20 individuals of each sex. A secondary sex character involves the ultimate (8 th) and penultimate (7 th) tergites (as for *Cryphalus* Erichson, Wood 1982, p. 42). In dorsal view, tergite 8 is visible in males whereas that of females is not visible because it is obscured by the enlarged tergite 7.

Table 1. *Trypophloeus striatulus* larval instar head widths and body lengths. Alaska, 1996–1997

Instar	n	Head width, mm		Body length, mm
		Average	Range	Range
I	20	0.27	0.25–0.29	1.0–2.5
II	20	0.35	0.34–0.39	2.0–2.8
III	20	0.45	0.42–0.51	2.7–4.0

Fig. 1. (A) In areas such as near Paxon, where moose were abundant, damage from browsing resulted in infection by a fungus and infestation by several generations of *Trypophloeus striatulus* followed by death of the affected stems. (B) Willows having stems killed by fungus and the beetle usually sprouted profusely as seen here along the Niukluk River.

Adult Behavior and Gallery Characteristics. New adults (F1) appeared in August. Females had undeveloped ovaries, and were therefore sexually immature. Both sexes walked for extended periods (none was seen to fly), probing the bark for a site to bore a "hibernation chamber" in which solitarily beetles over-wintered. A lenticel was chosen most often as a boring site, especially on areas of smooth bark, and beetles were observed to tap the lenticel surface with their antennae as though attracted there by an odor or other stimulus.

Over-wintered adults, however, were sexually mature. Females emerged from their hibernation chambers in late May and were joined by a male. Copulation occurred on the bark surface as described for *T. populi* by Petty (1977). Because there is usually no sizeable crevice in the bark, females lacked a mechanical purchase and stood at a high angle to begin boring their tunnel. Sometimes, however, they chose to enter an old hibernation chamber from which they constructed an egg gallery ≈4–7 mm long and 1.5–3.3 mm wide. Such egg galleries have been referred to in literature as "cave-type" (Wood 1982) and are primitive in comparison to those of many bark beetles that lay eggs individually along extended egg galleries, often in niches.

Eggs were laid in a cluster (Fig. 2) of as many as 36, but averaged ≈20 per female. First-instar larvae fed en masse. Subsequent instars fed separately; their larval mines extended up to 5 cm in length, usually becoming parallel with the trunk (Fig. 3). Their mines contained mostly excrement, formed into chains of pellets, and lacked fragments of phloem that are common in mines of many bark beetles. Nearing pupation, larvae chewed a pupal cell that shallowly scored the xylem surface, fragments of which then appeared among the frass.

Fig. 2. Primitive cave-type egg gallery exposed to show a beetle and a cluster of eggs.

Fig. 3. Ultimate, third-instar larvae at ends of their mines. After hatching, larvae aggregate to feed and then mine independently as they molt and grow, generally orienting their mines parallel to the trunk. The original egg gallery occupied the black area to left. Overlying brown phloem obscures the beginning of the four occupied larval mines.

Associated Organisms. Over-wintering larvae were excavated and eaten by unobserved birds, probably the hoary woodpecker or the three-toed woodpecker that occur in the areas where this was observed (Cantwell and SNWR). However, no insect parasite or predator was observed during the 1996–1997 studies in hundreds of galleries examined, although it was not uncommon to encounter a dead, outwardly undamaged, adult beetle in its hibernation chamber, the cause of which is unknown. My 1974 collection at Brushkana Campground did contain larvae of a pteromalid but its identity was not determined.

An unidentified, endoparasitic nematode occurred frequently in the hemocoele of apparently healthy adults. A sample of six infested beetles contained an average of 15 nematodes (4–40). They were 1.5 μ long.

Mites, presumed not to be predacious, were common in galleries, including the following taxa: Ascidae (*Proctolaelaps* n. sp., *P.* sp. near *scolyti* Evans.), Acaridae (*Histiostoma* sp.), and Anoetidae.

Maggots of the dipterous family, Sepsidae, were present in especially moist larval mines of mature beetle larvae. They are not predacious.

A thrips, *Acanthothrips nodicornis* Reuter (Phlaeothripidae), inhabited abandoned hibernation chambers and appears to over-winter there in the egg stage.

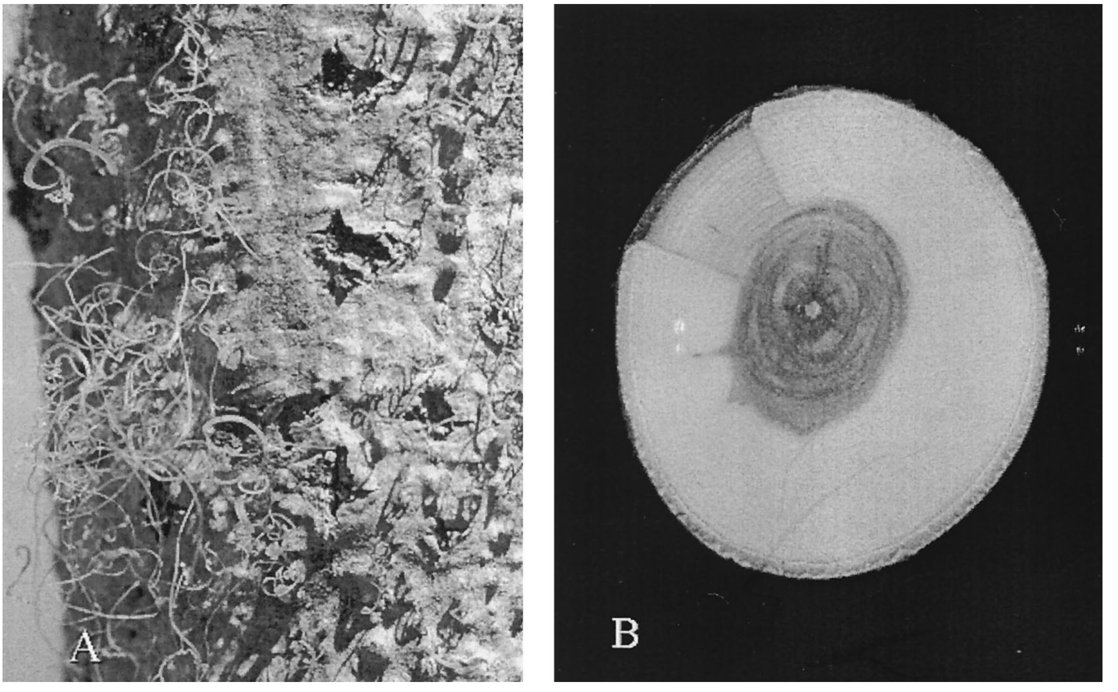

Fig. 4. (A) Thread-like, orange, tendrils of a pathological canker-forming fungus, *Cytospora* sp., associated with *Trypophloeus striatulus* in dying willow stems. The tendrils contain myriads of allantoid-shaped conidia. (B) Cross-section of a willow stem with brown-stained, wood inward of a canker in the bark. Cankers appear as longitudinal, sunken, areas on the bark. *Trypophloeus striatulus* and the fungus proceed slowly in stems for several generations of the beetle, which is adapted by its biology and behavior to conserving a limited resource of susceptible (damaged or senescent) feltleaf willow.

Infested stems contained evident cankers caused by *Cytospora* sp., probably *chrysosperma* (Person) Fries, although only its imperfect stage (that of *C. chrysosperma* is *Valsa sordida* Nitschke) was present and cannot be identified specifically. Symptoms of *Cytospora* infection consisted of longitudinal, sunken, necrotic areas (cankers) on bark, striated (ridged) bark, pustules (raised, pimple-like, mounds on bark), and eventually, orange, hair-like tendrils (Fig. 4A) consisting of strands of conidia, expressed under pressure from pycnidia (the pimple-like structures). Brownish staining occurred radially beneath lesions (Fig. 4B). This staining also developed inward from what appeared to be healed-over sapsucker injury.

Spores were visible on the pronotum of 11 of the 50 beetles examined by SEM but mostly in sparse numbers. The spores were 8 μ in diameter. These spores were most abundant behind tooth-like asperites that are present on the anterior half of the pronotum (Fig. 5A and B). Their identity is unknown but they are not conidia of *Cytospora* sp. that comprise tendrils and that are allantoid, not round, in shape and are $\approx$0.3 μ long.

Discussion

Several aspects of the beetle's biology and seasonal history were determined. One such aspect was the discovery that most broods transform to sexually immature adults and over-winter, solitarily, in hibernation chambers. Those chambers (comprising 90% of entrance holes on stems) had been thought to be unsuccessful attacks involving a plant-pathogenic fungus because of the formation of a woody ring around the chamber (Fig. 6). Formation of this ring is similar to the tylosing of cells surrounding those invaded by the fungus causing Dutch elm disease (Banfield 1968) isolating it from living phloem (defensive wound response). The beetle was not found to transmit *Cytospora* sp. but the wound response and presence of unidentified spores on the pronotum indicate that the beetle may carry a mutualistic fungus. Perhaps this organism requires a particular environment such as constant activity (e.g., mining, feeding) by reproducing adults and their progeny in order for it to succeed in extensively invading the phloem. The beetle's pronotum contains tooth-like asperites anteriorly and pits posteriorly (Fig. 5), making it well adapted to raking spores from the gallery backward to the pits and subsequently distributing them by their movements. Such adaptation has been shown for scolytids of the genus *Pityoborus* Blackman and their mutualistic fungi (Furniss et al. 1987).

Infection by *Cytospora* sp. and susceptibility to the beetle are closely linked, but the degree of interdependency is unclear. Although tendrils containing myriads of conidia form on beetle-infested feltleaf willow, they were not seen on beetles scanned by SEM. I have previously found spores of mutualistic ambrosia fungi and plant-pathogenic fungi carried on the integument of other scolytids (Furniss et al. 1987,

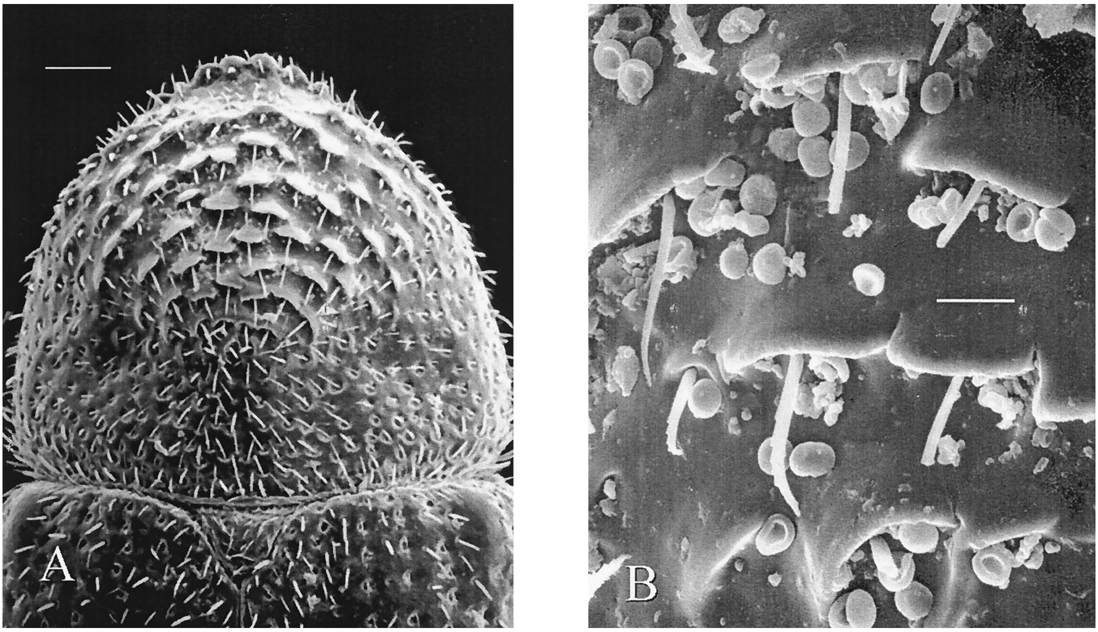

Fig. 5. (A) Pronotum of *Trypophloeus striatulus* with tooth-like asperites arranged in concentric rows on the anterior half (bar = 0.1 mm). (B) Magnified asperites, each with a seta, and unidentified spores deposited behind them. A similar organism may be involved in eliciting the defensive wound response that accompanies injury caused by beetles during excavation of hibernation chambers (bar = 12 μ).

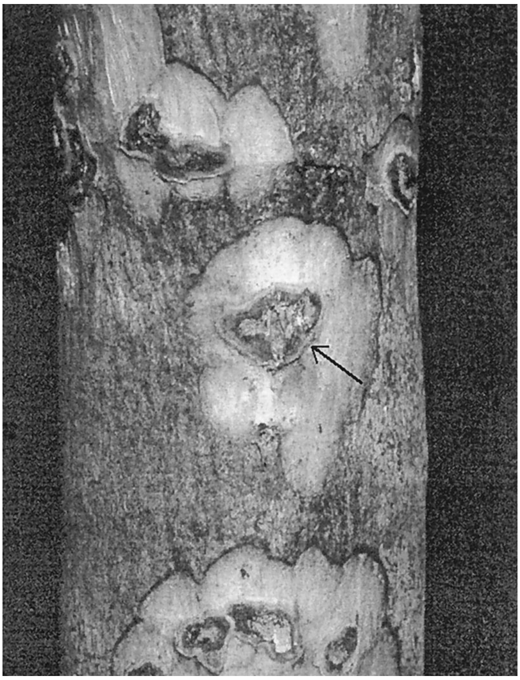

Fig. 6. Portion of willow stem with several hibernation chambers exposed by removal of overlying bark. Injury caused by boring these chambers results in tylosing of peripheral cells thereby isolating the surrounding live tissue. Note the distinct, woody, margin (arrow).

1990, 1995). Such means of vectoring this fungus does not appear necessary, however, because *Cytospora* spp. (including *C. chrysosperma*) readily infect willow and other plants that are injured (such as by browsing and ice jams in this case) or otherwise severely stressed (Boyce 1948, Hubert 1920).

Arrestment of beetles at lenticels may be because of an attractive odor diffusing through these porous, corky, areas. Lenticels are loosely arranged cells in the periderm that, because of the continuity of their intercellular spaces with those of inner tissues, probably have a function involved with gas exchange similar to stomata (Fahn 1990). Still unknown is whether an attractive odor exists and, if so, whether it originates with the fungus directly or indirectly (from diseased phloem), or other sources.

The study indicates that natural enemies are not important in regulating the population of this bark beetle in Alaska. Predacious birds may, however, exert selective pressure against the trait of over-wintering as larvae, opposed to over-wintering as dispersed, solitary, adults that provide slimmer pickings and that appear to escape such fate. What, then, is important in the population dynamics of this beetle? The answer lies in its biology and its host. *Trypophloeus striatulus* conserves a limited (susceptible) host resource by reinfesting rather than killing it in one generation, which would force it to disperse to another host. This adaptation involves walking dominance, low fecundity, and possibly attraction to odor emitted through lenticels that overlie susceptible fungus-infested phloem.

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